

Process-Specific Recruitment Cues in Marine Sedimentary Systems

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Abstract. In marine sediments, many of the processes associated with high post-settlement mortality of infauna have similar effects on the sediment surface. In most cases the original sediment surface is either removed, buried, or mixed with subsurface sediment. The experiments reported here tested the ability of new juvenile infauna to discriminate between undisturbed and recently disturbed sediment surfaces (*i.e.*, subsurface sediment exposed).

Recently settled juveniles of two polychaete species (*Nereis vexillosa* and *Arenicola cristata*) and one bivalve species (*Mercenaria mercenaria*) were exposed to simulated erosional and mixing events as well as to fresh feces, burrow tailings, and feeding tracks. Where the disturbance buried or removed several millimeters of the sediment surface, the time to initiate burrowing or the percentage of individuals failing to burrow increased significantly over times and percentages for juveniles on undisturbed surfaces. In all cases the results were consistent with the hypothesis that new juveniles reject (or are significantly slower to burrow into) disturbed sediment surfaces, if the disturbance is less than several hours old. For example, 51% of nereid juveniles did not burrow when placed on subsurface sediments, whereas 100% burrowed into surface sediments; their average burrowing time on surface sediments was 29.3 s compared with 109.7 s on fecal mounds of arenicolid polychaetes or 106.1 s on burrow tailings of thalassinid crustaceans. Individuals that did not indicate acceptance of a sediment surface by burrowing were all rapidly eroded from the surface in the presence of flow. Erosion of nonburrowing individuals occurred within 90 s of initiation of flow. Burrowing individuals were not eroded. The decision as to the acceptability of a sediment was made within 30 s. These data imply that

the new juveniles are utilizing cues associated with a process, the disturbance of surface sediments, in addition to the species-specific cues described elsewhere.

Introduction

Recruitment is of fundamental importance to community structure because it is the foundation upon which all subsequent interactions within the community take place. When recruitment fails, organisms do not have the opportunity to interact as adults (Underwood and Denley, 1984). Therefore, the often substantial variation in success of recruitment (Loosanoff, 1964; Wethey, 1985; Feller *et al.*, 1992) can profoundly influence the dynamics of adult populations. Two major classes of processes combine to determine the eventual recruitment success of species with planktonic larvae, assuming that competent larvae are in the plankton. First, larval transport on geographic and local scales can determine how many larvae actually reach a site and are retained (Boicourt, 1982; Cameron and Rumrill, 1982; Kendall *et al.*, 1982; Levin, 1984; Jonsson *et al.*, 1991). Only larvae that arrive on the bottom have an opportunity to exercise a behavioral choice of substratum (Highsmith, 1982; Butman *et al.*, 1988). Second, mortality and emigration occurring during or after settlement and metamorphosis can determine the success of the larvae that settle (Sellmer, 1967; Muus, 1973; Sigurdson *et al.*, 1976; Bell and Coull, 1980; Brenchley, 1981; Levin, 1981; Wilson, 1981; Watzin, 1983; Luckenbach, 1984; Connell, 1985; Wethey, 1985; Elmgren *et al.*, 1986; Woodin, 1986; Eyster and Pechenik, 1987; Walters, 1992). Thus, both presettlement and postsettlement events are involved in recruitment.

The literature on recruitment is dominated by two types of papers, those on mortality and those on larval choice. This dichotomy is interesting because the mortality literature is primarily directed toward elucidating how var-

Received 12 December 1994; accepted 2 May 1995.

Contribution Number 1051 of the Belle W. Baruch Institute for Marine and Coastal Research.

ious postsettlement factors cause greater mortality, *i.e.*, on negative influences. The literature on choice, if it were parallel, would be on cues by which new recruits avoid sites that have characteristics associated with high mortality. Instead, most of the choice literature is directed toward identification of positive, species-specific cues that are associated with the presence of either prey (Hadfield, 1984; Morse and Morse, 1984) or mates (Highsmith, 1982; Crisp, 1984). We would argue that given the cues associated with high mortality and the characteristics of recruits that allow them to recognize such cues, there would be strong selection for retention of individuals with such traits (for examples of larvae with such traits see Johnson and Strathmann, 1989, and Grosberg, 1981).

A characteristic common to the majority of the mortality sources for new juveniles in sediments, such as predation, erosion, and deposition, is that these mortality sources alter the sediment surface either by removing it or by covering it with a layer of subsurface or a mixed surface-subsurface. A testable deduction consistent with our proposed selection regime, then, is that new recruits distinguish between recently disturbed and undisturbed sediment surfaces. The experiments described here were designed to test this hypothesis. We confined ourselves to sediments that are stable and rarely move as bedload (for events characteristic of more mobile habitats, see Emerson and Grant, 1991). We defined the disruptions of interest to be those that either covered the original surface of the sediment or removed at least 3–5 mm vertically. Biotic erosional forces, such as tellinid bivalve feeding, and physical erosion can easily remove at least this much sediment. We also asked whether the behavior of new juveniles on disturbed surfaces is likely to result in rates of recruitment that are reduced compared with those on undisturbed surfaces.

Materials and Methods

Background information on infauna

New juveniles of infaunal bivalves and polychaetes were used to contrast the responses of taxa that can burrow as new juveniles (the polychaetes) and those that cannot (the bivalves). The use of new juveniles rather than settling larvae also avoids the potentially serious problem of differentiating between competent larvae and incompetent larvae of similar size and appearance (Bachelet *et al.*, 1992). Bivalves and polychaetes are quite different at the initiation of metamorphosis. For example, bivalves have a shell at settlement but usually cannot burrow for a week or more after metamorphosis begins (Belding, 1930; Carriker, 1961; Gustafson and Reid, 1986). Polychaetes lack a shell but can burrow at this developmental stage (Wilson, 1952; Roe, 1975). Bivalves generally cannot emigrate from a habitat by swimming off the bottom once their velum

has been lost; they can, however, both crawl and use water currents to waft away from a site after erosion off the bottom sediment (Sigurdsson *et al.*, 1976; Sastry, 1979). Many polychaete juveniles can crawl, waft, and actively swim away from a site, even after they metamorphose (*e.g.*, Roe, 1975). The important point of similarity is that sediment-dwelling juveniles of both taxa can crawl away as well as waft away. Thus rejection of a site may occur at the juvenile as well as the larval stage.

In all experiments, we used juveniles that had initiated metamorphosis less than one week before they were tested. The polychaetes were *Nereis vexillosa*, a nereid, and *Arenicola cristata*, an arenicolid. These larvae are lecithotrophic and were not fed. The juveniles of both species were fed *Isochrysis galbana* T-ISO strain as well as a mixture of diatom species. *Nereis* is common near the University of Washington Friday Harbor Laboratories on San Juan Island, Washington. Females lay egg masses containing hundreds of eggs (Johnson, 1943). *Arenicola* also lays egg masses that are initially attached to the bottom. Egg masses of both species were collected in the field and transported to the laboratory, where they were placed in individual micro-airlifts (Strathmann, 1987) until the larvae hatched at four to five setigers (*Nereis*) or three to four setigers (*Arenicola*). Swimming larvae were cultured in 11-cm-i.d. glass culture dishes. When the larvae develop six setigers, at a length of about 500 μm for *Nereis* and about 600 μm for *Arenicola*, the larvae will burrow and build tubes in acceptable sediments. Both polychaete species actively reject some sediments by either initiating a crawling sequence or standing perpendicular to the sediment surface, attached only by a mucus thread. In flowing water such individuals are easily eroded off their attachment point (see below). Sediments into which the recruits did not burrow within the observation period were classified as unacceptable.

The bivalve species used in these experiments was *Mercenaria mercenaria*. Late pediveligers of *Mercenaria* were cultured in the laboratory with stirring and fed *Isochrysis galbana* T-ISO strain until settlement and initiation of metamorphosis. The individuals of *Mercenaria* averaged 0.307 mm (SD = 0.035) in length. New spat of *Mercenaria* do not penetrate the sediments and burrow; rather they nestle into the substratum to about half the length of the shell, position themselves with the hinge down, and gape slightly (Carriker, 1961). Initiation time for spat was defined as the time at which the foot of the individual penetrated the sediment surface and the shell was pulled down. In some types of sediments the spat fail to show this nestling behavior; instead they remain on the surface, typically resting on one valve or sometimes actively crawling across the sediment without any evidence of movement of the hinge and shell below the sediment sur-

face. Sediments eliciting such behaviors were classified as unacceptable.

Behavioral observations

Glass dishes with a 1.5- to 2-cm layer of test sediment on the bottom, covered by a layer of seawater 2 cm deep, were used for observations. Individual juveniles were gently pipetted into the water column and allowed to drift onto the sediment surface. Individuals that contacted the sediment surface forcefully, landed on a sand grain larger than their length, or (for the worms) landed in any position other than their ventral surface were not used in the analyses. Timing of responses to the sediments began when the individual made contact with the sediment surface. A dissecting microscope was used to monitor individuals continuously from their arrival on the sediment surface until they disappeared below the surface (polychaetes) or nestled in among the surface sediments and began to feed (bivalves), or until the designated observation period expired. The length of the observation period depended upon the species (*Nereis*, 5 min; *Mercenaria*, 6 min; *Arenicola*, 7 min) and was set to a minimum of 10× the mean time individuals took to initiate burrowing in preliminary observations. In the experiments with *Nereis* and *Mercenaria*, 4 to 10 individuals were separately added to each dish or core. To avoid the possibility of interactions, individuals that landed within 2 cm of another animal were not used.

Experimental sediments

Experimental sediments were collected in the field and immediately transported to the laboratory. Sediments were collected as two types: surface sediments (the top 1- to 2-mm-thick layer) and subsurface sediments (the 1- to 2-mm-thick layer exposed after removal of the top 4 to 5 mm). In the field, the surface sediments were collected with a paint scraper. Areas of disturbance such as fecal mounds, burrow scrapings, tubes, and feeding traces were avoided. Subsurface sediments were collected by removing the top 4 to 5 mm of sediment and then collecting the next 1 to 2 mm with a paint scraper. In field-processed sediments, each type of sediment was collected and placed in a 11-cm-i.d. glass dish, creating a layer 1.5 to 2.0 cm deep. Once in the laboratory, each dish was filled with seawater to a depth of at least 2 cm. Dishes were stored floating in a seawater table and were used within 2 h. In addition, we used several other types of sediments: fresh feces of arenicolid polychaetes (*Abarenicola pacifica*), fresh burrow scrapings of thalassinid crustaceans (*Upogebia pugettensis*), 1:1 mixtures by volume of surface and subsurface sediments, and sediments that had been reworked physically by storm events. All were used within 2 h of

collection, including the 1:1 mixtures that were made from field-collected sediments.

Juvenile *Nereis* were also tested on sediments containing active macrofauna. Sediments from False Bay were defaunated by freezing, thawing, and refreezing, then rinsed thoroughly with seawater and sieved on a 0.5-mm mesh. Cores (7 cm × 6 cm i.d.) of defaunated sediment were either inoculated with known numbers and species of macrofauna or left as controls. After two weeks, juvenile *Nereis* were exposed to the surfaces of each type. Within the macrofauna-addition cores, the juveniles were added to the feeding areas of the macrofauna (half of the tested cores) as well as to sites outside of the feeding areas (remainder of the macrofauna-addition cores). The macrofauna used were three species of spionid polychaete (*Spio* sp., *Rhynchospio glutaeus*, and *Pygospio elegans*) and a tellinid bivalve (*Macoma nasuta*).

Several sites were used for sediment collection. In all cases adults of the species to be tested were common at the collection site. For *Nereis vexillosa* the sites were a semiprotected fine sandflat, False Bay, Washington (48°29' N; 123°04' W, median grain size 0.18 mm, silt-clay 10%) and a more enclosed bay with a mud-gravel sediment mixture, Snug Harbor, Washington (48°34' N, 123°10' W, median grain size 1.66 mm, silt-clay 6%). For *Arenicola cristata* and *Mercenaria mercenaria* the sites were medium- to fine-grained sandflats on the landward side of Pawleys Island, South Carolina (33°24' N, 79°8' W, median grain size 0.39 mm, silt-clay 0.05%) and at Oyster Landing, North Inlet, South Carolina (33°20' N, 79°12' W, median grain size 0.38 mm, silt-clay 0%). The numbers of replicates per treatment differed among experiments and are given in the Results section.

All experiments on *Nereis vexillosa* were run in June 1990 at the Friday Harbor Laboratories. The controls were run on every day of the experiment, and each experimental treatment was run on most days. The experiments on *Arenicola cristata* were run in July 1992. Those on *Mercenaria mercenaria* were run in May 1991. Controls were always alternated with experimental sediments to ensure that the juveniles were still responsive.

Flume observations and design

A rectangular pipe flume, 1.3 × 10 cm in cross section and 1.26 m in length, was fitted with a 2.5 × 2.5 cm sediment box 0.8 m from the inlet. Honeycomb material (5-mm cells, 11 cm long) was used as a flow straightener in the inlet. A hot film flow sensor (TSI 1231W) was flush-mounted 0.5 cm upstream from the test section. The sensor was calibrated in the wall of a cylindrical pipe. The flume geometry is scaled up from the larval flume used by Eckman *et al.* (1990) in their studies of barnacle cyprids. Rectangular pipe flow was turbulent, with boundary

layer growth from the top, bottom, and sides of the flume. The test section was small enough that flow characteristics varied by no more than 10% over its area. The flow near the sediment surface can be summarized by the boundary shear velocity u_* , which is a measure of the turbulent momentum transfer from the water to the sediment, and is calculated from the covariance between the vertical (v) and horizontal (u) velocity fluctuations:

$$u_* = \sqrt{\text{cov}(u, v)}$$

In our flow treatments the boundary shear velocity was approximately 1.0 cm s^{-1} , which is close to the critical erosion condition for sediments in False Bay (critical erosion $u_* = 1.2 \text{ cm s}^{-1}$; Miller and Sternberg, 1988). In our flow treatments, which are typical of tidal flows, surface sand grains wiggled and surface floc was eroded. In storms with 15-cm waves, u_* can be 3.5 cm s^{-1} or higher, and large amounts of sediment are resuspended (Miller and Sternberg, 1988).

Individual juveniles were introduced to the flume through an opening about 1 cm upstream of the test section. As in the still-water dish experiments, individuals were timed from the moment of initial contact with the sediment surface. A dissecting microscope with a video camera was used to observe the behavior of six-setiger *Nereis* juveniles on sediments of three types: surface sediments of False Bay origin; clean, not previously seawater-aged, foundry sand; and surface sediments of False Bay origin contaminated with the dibromobenzyl alcohol produced by the terebellid polychaete *Thelepus crispus*. Contaminated sediments resulted from introducing *T. crispus* into the sediments for a minimum of 48 h (for concentration data as well as extraction details, see Woodin *et al.*, 1993). Such sediments are known to be rejected by juveniles of *Nereis* in both the field and the laboratory (Woodin *et al.*, 1993). In most cases, juveniles were observed in still and flowing water.

Statistical analysis

All experiments were analyzed using PC SAS version 6.04 (SAS Institute, Cary, NC). The data were of two types: (a) times to initiation of burrowing or nestling and (b) percentages of juveniles per dish accepting or rejecting the sediment. In the first case only individuals that initiated burrowing or nestling were used. The burrowing times were analyzed by analysis of variance (*Arenicola*) or nested analysis of variance with dishes nested under treatment (*Nereis* and *Mercenaria*). If a large number of the individuals failed to initiate burrowing, making the number of observations per dish per treatment highly unbalanced, then the analysis was done on the average time to initiation of burrowing for each dish. In these cases, the analysis was not nested. Simultaneous comparisons

among treatments were made with the Tukey's studentized range test. All data were examined for normality and homogeneity of variance and transformed if necessary. The analyses and transformations used are indicated for each experiment below. The percentage burrowing data for the nereid juveniles were normalized using an arcsine square root transformation and analyzed by analysis of variance followed by an *a posteriori* Tukey's studentized range test, except for the data from Snug Harbor. Those data were non-normal with unequal variances per treatment, so the data were analyzed by separate Fisher's exact tests using a conservative probability of 0.01. For the data on *Mercenaria* and *Arenicola* juveniles where only two treatments were involved, a Fisher's exact test was used.

Results

Juveniles on field-collected sediment

When sediment from a semiprotected fine sand site (False Bay, WA) was used, juveniles of *Nereis vexillosa* clearly differentiated between surface and subsurface layers: 100% burrowed into surface sediments and 51% burrowed into subsurface sediments (Table 1: False Bay—Calm). The same was true for 1:1 mixtures by volume of surface and subsurface sediments; 25% failed to burrow within the 5-min observation period. In contrast, the rejection rates were only 12% and 14% for freshly collected burrow cleanout sediments of thalassinid crustaceans (burrow tailings) and arenicolid polychaete feces, respectively. The percentages of juveniles rejecting the sediment were significantly greater for the subsurface and 1:1 mixture treatments than for the surface, feces, and burrow tailings (ANOVA, arcsine square root transformation: $df = 4, 19$; $MSE = 0.0599$; $F = 6.39$; $p < 0.005$; multiple comparison tests: Table 1). For individuals that did burrow, times to initiate burrowing were significantly shorter on undisturbed surface sediments than on all treatments including naturally disturbed sediments (ANOVA, reciprocal transformation of average times per dish: $df = 4, 19$; $MSE = 0.00017$; $F = 6.10$, $p < 0.005$) (Table 1: False Bay—Calm).

The surface *versus* subsurface trials were repeated with juveniles of *Nereis* in a mud-gravel mixed sediment (Snug Harbor, WA). The results were similar to those for the fine sand habitat (False Bay, WA). One hundred percent of the nereid juveniles burrowed into the surface sediments, but only 50% burrowed into the subsurface sediments. For individuals that did burrow, times to initiate burrowing were significantly shorter in all treatments other than the subsurface sediments (Table 1: Snug Harbor) (ANOVA, average times per dish: $df = 3, 6$; $MSE = 79.53$; $F = 40.29$, $p < 0.0005$). Because of resuspension problems,

Table 1

Responses of nereid juveniles to selected sediment types: Part A, rejection percentages by dish; Part B, initiation times in seconds of individuals that burrowed

Part A. Percentage of Individuals That Did Not Burrow						
Sediment	False Bay—Calm		False Bay—Storm		Snug Harbor—Calm	
	N	Reject	N	Reject	N	Reject
Surface	45	0 (0) A	10	0 (0) A	40	0 (0) A
Subsurface	31	51 (12) B	8	0 (0) A	30	50 (26.5) B
1:1 mix	39	25 (7) B	NA	NA	NA	NA
Feces	50	14 (8) A	NA	NA	21	0 (0) A
Bur. tailings	50	12 (6) A	NA	NA	20	0 (0) A

Part B. Initiation Times (s) of Individuals That Burrowed						
Sediment	False Bay—Calm		False Bay—Storm		Snug Harbor—Calm	
	N	Init. (s)	N	Init. (s)	N	Init. (s)
Surface	45	29.3 (3.8) A	10	58.4 (21.6) A	40	15.3 (3.8) A
Subsurface	15	126.6 (11.0) B	8	41.8 (6.8) A	15	97.8 (5.9) B
1:1 mix	30	117.6 (25.7) B	NA	NA	NA	NA
Feces	43	109.7 (19.5) B	NA	NA	21	25.2 (10.3) A
Bur. tailings	44	106.1 (24.3) B	NA	NA	20	31.6 (3.5) A

'1:1 mix' are volumetric mixtures of surface and subsurface sediments; 'feces' are fresh feces of the polychaete *Aharenicola pacifica*; 'bur. tailings' are fresh burrow cleanouts of the thalassinid crustacean *Upogebia pugettensis*. 'Reject' is the mean percentage of individuals per dish which did not burrow. 'Init. (s)' is the time in seconds to initiation of burrowing into the sediment. These are means and standard errors of individuals by dish. 'NA' means not available. Letters after each number indicate the results of *a posteriori* Tukey's studentized range tests ($p \leq 0.05$) for that column category, with the exception of the percent rejection data for Snug Harbor, which are Fisher's exact tests. Numbers with the same letter within a column are not significantly different from one another. False Bay is a semiprotected, muddy sand site, while the sediment at Snug Harbor is a protected mud-gravel mixture. 'False Bay—Storm' are results from False Bay sediments following a windstorm that caused whitecaps within the bay. 'N' is total number of juveniles used in that treatment.

we were unable to make satisfactory 1:1 mixtures of the sediments at this site.

The results for time to initiate burrowing for the juveniles of *Arenicola cristata* were similar to those for *Nereis vexillosa*. The time to initiate burrowing was significantly longer for juveniles on subsurface sediments than on surface sediments (ANOVA, log transformed times: $df = 1, 21$; $MSE = 0.0497$; $F = 26.97$; $p < 0.0001$) (Table IIB). The percentage burrowing into each treatment was equivalent: 93% burrowed into surface sediments; 86% burrowed into subsurface sediments.

New juveniles (spat) of *Mercenaria mercenaria* clearly differentiated between surface and subsurface sediments, both in mud and sand (Table IIA). The initiation times were significantly shorter on surface sediments than on

subsurface sediments (nested ANOVA, log base 10 transformed data: $df = 1, 4$; $MSE = 0.064$; $F = 39.4$; $p < 0.005$) (Table IIA). Correspondingly, for both mud and sand sediment combined, 100% nestled into surface sediments, but only 40% to 50% nestled into subsurface sediments (Table IIA). The initiation times were not significantly different between mud and sand sediments (nested ANOVA, log base 10 transformed data: $df = 1, 24$; $MSE = 3.13$; $F = 0.08$; $p = 0.78$). Particle size appears to be much less important than whether the sediment is from the surface or the subsurface.

Storm-mixed sediments

At one of our sites, False Bay, storms have been observed to resuspend and transport surface sediment layers at a rate of $16 \text{ mg cm}^{-2} \text{ s}^{-1}$ (average sediment flux rate without regard to direction) and $5.4 \text{ mg cm}^{-2} \text{ s}^{-1}$ (deposition or vertical sediment flux rate) (Miller and Sternberg, 1988). When a storm occurred during these experiments, we collected surface and subsurface sediments and exposed the nereid juveniles to them. As expected under these conditions—surface and subsurface sediments thoroughly mixed to a depth of several centimeters—there was no significant difference in time to initiate burrowing on surface compared with subsurface sediments (Table I: False Bay—Storm: nested ANOVA: $df = 1, 6$; $MSE = 1578.48$; $F = 0.65$; $p = 0.45$). One hundred percent of the nereid juveniles burrowed into the surface and the subsurface sediments. This result is quite different from that obtained with 1:1 mixtures of sediment in which subsurface sediment was mixed with surface sediment without the agitation and aeration typical of storm-induced sediment mixing.

Feeding traces

Juvenile *Nereis* were also tested on sediments containing active macrofauna: the spionid polychaetes *Spio* sp., *Rhynchospio glutaeus*, and *Pygospio elegans* and the tellinid bivalve *Macoma nasuta*. Individuals of each species were introduced into separate cores of defaunated sediment and maintained in the laboratory in running seawater for two weeks before use. Only cores with obvious feces after the two-week incubation were used. Controls were cores without added fauna; these control cores were also maintained in running seawater in the laboratory for two weeks before use. Although 100% of the nereid juveniles burrowed in all treatments, times to initiate burrowing were significantly different among the treatments (nested ANOVA on log transformed data: $df = 7, 16$; $MSE = 0.0883$; $F = 18.76$; $p < 0.0001$). The feeding traces of *Macoma* caused a significant increase in time to initiation of burrowing (Table IIIA). Of the species tested, *Macoma* is the infaunal organism with the deepest feeding

Table II

Times in seconds to initiate nestling or burrowing into the sediment ('Init. Time') by juveniles of *Mercenaria mercenaria* and *Arenicola cristata*

Sediment	Type	N	Init. Time	N	Perc. Reject	
<i>Mercenaria mercenaria</i>	Surface	10	35.7 (7.7) A	10	0 (0) A	
	Mud	5	156.6 (35.5) B	10	50 (50) B	
	Muddy sand	Surface	10	21.7 (6.7) A	10	0 (0) A
		Subsurface	6	128.4 (7.1) B	10	40 (20) B
<i>Arenicola cristata</i>	Surface	13	41.4 (6.4) A	14	7 A	
	Muddy sand	12	133.9 (23.2) B	14	14 A	

Percentage of the individuals that did not nestle or burrow within the observation period ('Perc. Reject'). Letters after each number indicate the results of a *posteriori* Tukey's studentized range tests ($p \leq 0.05$) for initiation times in seconds ('Init. Time') or a Fisher's exact test for percentage rejecting the sediment ('Perc. Reject'). Numbers with the same letter are not significantly different from one another. 'N' is number of juveniles in that treatment. Means and standard errors are for individuals by dish for *Mercenaria mercenaria* and by treatment for *Arenicola cristata*.

traces: 2 to 5 mm compared with 1 mm or less for the spionid polychaetes.

Times to burrow were significantly greater on recent feeding traces than in adjacent areas (nested ANOVA on log transformed data; $df = 3, 32$; $MSE = 0.1132$; $F = 5.33$; $p < 0.01$) (Table IIIB). The distances between sites of different types on a single core surface were 3 cm or less, showing that differentiation can occur on small spatial scales.

Table III

Times in seconds ('Init. Time') for juveniles of *Nereis vexillosa* to initiate burrowing

Macrofauna	Type of Location	Init. Time	N	
Part A.				
	<i>Spio</i> (P)	Control	7.3 (0.7) A	15
		Feeding	8.3 (1.0) A	15
<i>Pygospio</i> (P)	Control	15.1 (3.4) A	15	
	Feeding	7.3 (1.6) A	16	
<i>Rhynchospio</i> (P)	Control	10.4 (2.7) A	15	
	Feeding	10.7 (2.0) A	17	
<i>Macoma</i> (B)	Control	14.6 (1.9) A	20	
	Feeding	59.5 (19.6) B	22	
Part B.				
<i>Macoma</i> (B)	Outside recent disturb.	24.5 (6.8) A	17	
	New feeding areas	59.5 (19.6) B	22	

Means and standard errors of initiation times by core. Part A. Results from core surfaces with known macrofauna present, feeding areas only ('feeding') or from surfaces of cores held in the same tank but without macrofaunal additions ('control'). Part B. Results for cores with *Macoma*, different locations within the same core. All cores with *Macoma* added but sites designated as recently disturbed or undisturbed. Recently disturbed sites were areas of recent feeding activity by *Macoma*. The surface floc layer was missing and the feeding traces were clearly defined. Letters in parentheses after the species indicate taxon: 'P' polychaete and 'B' bivalve. Letters after each number indicate the results of a *posteriori* Tukey's studentized range tests ($p \leq 0.05$) for that column category within that section of the table. 'N' is total number of juveniles used in that treatment.

Flow versus no-flow conditions

In the flume with surface sediments as the test substrate, times to initiate burrowing by *Nereis* juveniles were similar for still water and flow treatments (Table IV: Burrowed: Init.), and burrowing individuals were not eroded from such surfaces. All but 3 of 17 juveniles successfully burrowed in the flow treatment; all burrowed without flow (Table IV). In the flow treatment, flow was initiated as soon as the individual appeared to reach the sediment surface. The three that were eroded blew off at 2, 3, and 135 s. The first two probably had not made contact with the sediment surface before flow was initiated.

Observations were also made on individuals placed onto sediments likely to be unacceptable to the nereid juveniles: clean foundry sands and sediment contaminated with the bromobenzyl alcohol of *Thelepus crispus* (Woodin *et al.*, 1993). The nereids did not burrow immediately on either of these sediments; in contrast, on uncontaminated surface sediments, the nereid juveniles burrowed on average within 11 s both with and without flow (Table IV). To ensure that individuals had made contact with the sediment surface in the treatments with foundry sand and with contaminated sediments, flow was not initiated until at least 20 s after the juveniles made contact with the sediments. Individuals remaining on the surface for more than 40 s were eroded within 2 min in all but 3 of 17 cases. One of the three eventually burrowed (at 210 s), while the other two eroded off. Times to erosion once flow was initiated are given in Table IV. On average, individuals were eroded in less than 80 s with flow (Table IV: Erosion Time in Flow).

Discussion

Surfaces of sedimentary habitats are dynamic landscapes, changing in response to both biotic and physical forces. Currents, winds, and waves can mix, resuspend, transport, move as bedload, and deposit sediments, al-

Table IV

Responses of nereid juveniles to selected sediment types in the flume

	Burrowed		Eroded			
	N	Init. (s)	N	Seconds	Erosion time in flow	Perc. reject
Surface Sed.						
No flow	7	9.8 (14.7) A	0	NA	NA	0 A
Flow	14	10.4 (5.8) A	3	46.7 (76.5)	46.7 (76.5)	17.6 A
All with Flow						
Surface sed.	14	10.4 (5.8)	3	46.7 (76.5) A	46.7 (76.5) A	17.6 A
Foundry sand	0		8	170.1 (135.3) B	80.7 (96.8) A	100 B
Thelepus sed.	1	210	9	51.3 (17.5) AB	15.9 (15.2) A	90.0 B

'Burrowed' means those individuals that burrowed into the sediment. 'Init. (s)' is the time in seconds to initiation of burrowing into the sediment. 'Eroded' is the time in seconds from contact with the sediment surface to erosion and includes both time with and without flow. 'Erosion Time in Flow' is the time in seconds from initiation of flow to erosion off the surface. 'Perc. Reject' is the percentage of the individuals that did not burrow. 'N' is the number of juveniles per category of a treatment. 'NA' means not available. For example, in the no-flow treatment for surface sediments, 7 juveniles burrowed, none were eroded, and 0% rejected the sediment. Letters after each number indicate the results of a *posteriori* Tukey's studentized range tests ($p \leq 0.05$) for that column category with the exception of 'Perc. Reject', which are results of Fisher's exact tests. Numbers with the same letter within a column are not significantly different from one another at the 0.05 level. Means and standard deviations are given.

tering the landscape (Miller and Sternberg, 1988). Biotic events such as predator excavations, surface deposit feeding, pit feeding, burrowing, and defecation also shape the sediment surface (Hughes, 1969; Rhoads and Young, 1970; Brenchley, 1981; Grant, 1983; Smith *et al.*, 1986; Nowell *et al.*, 1984; Posey, 1986; Krager and Woodin, 1993). Many of these events require a response from the infauna. Sediment deposition, whether biotic or physical in origin, can result in a period of burrowing and reestablishment or even in the death of the infauna (Gallucci and Kawaratani, 1975; Nichols *et al.*, 1978; Turk and Risk, 1981; Wilson, 1981).

Recently settled juveniles of infauna are particularly susceptible to a number of these surface-associated processes. Feeding by surface deposit-feeders, such as spionid polychaetes and tellinid bivalves, can result in spatial partitioning of large individuals (Holme, 1950; Levin, 1981) or mortality of small ones (Wilson, 1980; Levin, 1981; Elmgren *et al.*, 1986; Hines *et al.*, 1989; Olafsson, 1989). Sediment deposition can also increase rates of mortality for juveniles (Wilson, 1981; Brenchley, 1982; Posey, 1986). These biotic and physical events have similar effects on the original sediment surface, causing either burial or removal of the original surface. Given this commonality of effect on surfaces and on mortality rates, selection should favor those recruits capable of (a) distinguishing between recently disturbed (exposed subsurface sediments) and undisturbed surfaces and (b) emigrating from sites with disturbance. The data presented here show clearly that new juveniles of two polychaete species and a bivalve species can distinguish between recently disturbed and undisturbed sediment surfaces and modify their behavior accordingly. In all cases, burrowing times

are significantly greater on recently disturbed surfaces than on undisturbed surfaces (Tables I to III); in some cases, rates of complete rejection, where the juvenile did not burrow, are higher on disturbed surfaces (Tables I and II). This was true for simulated erosional events (surface compared with subsurface: Tables I and II), as well as for simulated mixing (surface compared with 1:1 mix: Table I). Time to acceptance was also significantly longer for new juveniles offered fresh feces or burrow tailings than for those given undisturbed surface sediments (Table I). Finally, exposure to feeding traces made by large infauna such as the tellinid bivalve *Macoma nasuta* caused significant increases in burrowing times (Table III). All of these results are consistent with the hypothesis that juveniles distinguish between undisturbed and recently disturbed sediment surfaces, whether the disturbance is depositional or erosional, physical or biotic. A corollary of this hypothesis is that there is a selective advantage to individuals able to distinguish between recently disturbed and undisturbed sediment surfaces. This does not, of course, mean that the currently undisturbed site will remain undisturbed, either by biotic or physical forces (Wilson, 1981; Krager and Woodin, 1993).

When disturbed sediments were accepted by the juveniles, times to initiation of burrowing or nestling were significantly (4- to 5-fold) longer than in undisturbed sediments (Tables I and II). Under these conditions, juveniles remained on the sediment surface for 1.5 to 2 min or more. Such behaviors can increase the probability of erosion. Our flume data clearly indicate that individuals that did not burrow were eroded (Table IV). None of the individuals that burrowed was eroded. All but 3 of the 17 individuals that did not burrow within 40 s of contacting

the bottom were eroded within 2 min of initiation of flow. On average, erosion of individuals from the surface occurred in less than 80 s after initiation of flow. Flow in these experiments had an average boundary shear velocity of 1.0 cm s^{-1} , which is much less than storm conditions (False Bay, WA: $u_* = 3.5 \text{ cm s}^{-1}$ or more; Miller and Sternberg, 1988) and is comparable to conditions for maximum flood tidal flows [Oyster Landing, SC: u_* : 0.7 to 1.0 cm s^{-1} (Palmer and Gust, 1985; Wetthey *et al.*, unpub. data)] in these habitats or for small-amplitude waves (Denny and Shibata, 1989). Thus our flume results are a highly conservative estimate of the probability of erosion. Interestingly, the temporal spacing between small-amplitude waves typical of these habitats and likely to cause erosion is of the same order of magnitude as the time necessary to initiate burrowing (Pond and Pickard, 1983; Denny, 1988; Miller and Sternberg, 1988).

Travel by erosion or wafting is a well-known phenomenon (Sigurdsson *et al.*, 1976; Sastry, 1979) and may also help explain some of the results of Butman and her collaborators on the effect of still water and flow conditions on larval settlement selectivity (*e.g.*, Snelgrove *et al.*, 1993). Some species show more settlement selectivity with flow than without (*Mulinia lateralis*: Grassle *et al.*, 1992b), whereas other species are relatively insensitive to the presence or absence of water motion (*Capitella* sp. 1: Butman and Grassle, 1992; Grassle *et al.*, 1992a). For species that rely on erosion from the surface to transport them short distances, such as the nereid juveniles used in these experiments, the no-flow treatment would result in lowered rates of emigration and thus less apparent selectivity.

Larvae and new juveniles are known to reject other habitats on the basis of chemical cues (see review by Pawlik, 1992), although the literature on negative settlement cues is not extensive. In all of these cases, the compound that causes rejection is intimately associated with the organism and is produced by that organism or a symbiont. For example, the terbellid polychaete *Thelepus crispus* releases a brominated aromatic compound into the sediments surrounding its tube, and this inhibits the recruitment of *Nereis vexillosa* (Woodin *et al.*, 1993). To date, all the reported negative responses are to organism-specific cues (Pawlik, 1992). In the data reported here, the negative response is to a process-specific event, disruption of the surface sediments either by removal or burial (Tables I to III). A process-specific cue is distinctly different from an organism-specific cue. For example, although a number of organisms have bioactive compounds that deter settlement, these compounds vary greatly in their effectiveness on different taxa, and the effect of the compound is typically limited to the surface of the organism itself or the immediately surrounding area (Pawlik, 1992; Woodin *et al.*, 1993). With process-specific cues, the effect is confined to the area affected by the process, which can be physical

or biotic, and is thus not limited to the distribution or abundance or even the habitat of a given taxon. Given the mortality associated with sediments that are disturbed, the selective advantage accrued to individuals able to differentiate between disturbed and undisturbed habitats and vary emigration rates in response is potentially enormous.

Acknowledgments

Dr. Mark Luckenbach kindly provided late pediveliger *Mercenaria mercenaria* larvae. The Director of the Friday Harbor Laboratories gave us research space and access to research sites. The Snug Harbor Resort allowed us to use their property as a research site. The Director of the Belle W. Baruch Institute for Marine and Coastal Research allowed us access to research sites. E. R. W. Wetthey collected egg masses and provided field assistance. C. Richmond, M. Grove, J. Hilbish, L. Levin, W. H. Wilson, R. Zimmer-Faust, and two anonymous reviewers made valuable comments on the manuscript. S. M. Lindsay was supported by an NSF graduate research fellowship. This research was supported by NSF grant OCE-8900212 to S. A. Woodin and ONR grant N00014-82-K-0645 and NSF grant OCE-86-00531 to D. S. Wetthey.

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